# Geographic Variation in the Black Rhinoceros Diceros bicornis (L., 1758)

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The systematics of the Rhinoceroses have been badly neglected in the present century as a whole. There has been no revision of the family Rhinocerotidae, although the interrelationships of living and fossil forms are in constant dispute. Nor has there been much infrageneric taxonomy; only in the past few years has interest seemed to revive in the group. The present author (in press) has attempted a revision of the South-east Asian species *Rhinoceros sondaicus* and *Didermocerus sumatrensis*, although with the rather small amount of material available this must of necessity be tentative. The only really major work has been that of ZUKOWSKY (1964) on the African species *Diceros bicornis*, the Black Rhinoceros. This has certain drawbacks, but these concern interpretation rather than fact, and as a reference work on aspects of nomenclature, observed variability, distribution etc. it will stand as the source-book on the species for years to come.

Having said this, however, one must proceed to criticise the taxonomic philosophy involved. From a wealth of photographs of living animals and skulls, and from the measurements of 79 skulls, the author felt able to recognise no fewer than sixteen subspecies, as well as a "variety", of which eight were described for the first time. Taking the skull measurements — undeniably the most important line of evidence, if only because subjectivity is absolutely ruled out — this gives an average of just under five skulls per subspecies. When closely examined, the skull measurements do not discriminate between the different forms in many cases, and one is left dependant upon the much more subjective assessment of the photographs to substantiate the forms described.

MERTENS (1966) has already pointed out that three of the names given by ZUKOWSKY have no nomenclatorial status as they were proposed by implication and thus invalid according to the International Code of Zoological Nomenclature, XV congress. Two of these names were based on one skull each; and the third was based on two photographs of freshly-shot specimens. One must always regret the erection of new races on such insecure evidence.

It is for two reasons that the present study is offered: first, for the reason that the taxonomic ideas of ZUKOWSKY will not find ready acceptance among the majority of modern workers; and secondly because a number of specimens not seen by ZUKOWSKY have been studied by the present author. These specimens are from the Powell-Cotton Museum (Birchington, Kent, England), the Copenhagen Zoological Museum, the Royal College of Surgeons, the Cambridge Zoology Museum, the American Museum of Natural History and the Smithsonian Institution (U.S. National Museum). Also, many of the specimens in ZUKOWSKY's list have been seen by the present author, and the technique of measurement checked; and some additional specimens in London, Munich and Vienna have been seen which were not mentioned in the list. (The London specimens in his table are from measurements by HOPWOOD and SCHWARZ, and the Munich and Vienna ones by TRUMLER; in the first case, the museum has received

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# Table 1

# Means and standard deviations for population groupings of Diceros bicornis.

Means only are given where the figure is based on under four specimens. Figures in parenthesis indicate that only one specimen could be measured.

	Greatest length	Basal length	Zygomatic breadth	Toothrow length	Occiput breadth
1. East African ar	еа				
Karagwe (4) Serengeti (3) Eyasi area (12) "Arusha" (3) Kilimanjaro (3) Tsavo (6) Kiboko (4) Tana river (3) Lakiundu R. (3) Aberdares (4) Baringo (2) N. Guaso	$586.7 \pm 22.5$ 566.7 $557.2 \pm 22.7$ 570.5 559.5 $542.8 \pm 15.7$ $546.3 \pm 14.9$ 523.3 557.0 $567.5 \pm 12.6$ 594.5 $578.8 \pm 16.5$	$\begin{array}{cccc} 534.7\pm&8.3\\ 546.3\\ 525.8\pm14.8\\ 547.0\\ 518.5\\ 527.5\pm15.3\\ 521.0\pm5.8\\ 507.7\\ 534.3\\ 546.7\pm&6.2\\ (542.0)\\ \\ 550.3\pm&9.7\\ \end{array}$	$\begin{array}{c} 329.8 \pm 11.6 \\ 329.0 \\ 327.0 \pm 12.8 \\ 332.0 \\ 332.7 \\ 332.2 \pm 9.0 \\ 326.8 \pm 7.9 \\ 319.7 \\ 327.3 \\ 335.8 \pm 6.8 \\ 347.5 \\ 334.8 \pm 10.4 \end{array}$	$\begin{array}{c} 252.5\pm10.7\\ 263.5\\ 256.9\pm9.0\\ 254.0\\ 245.3\\ 264.0\pm13.8\\ 244.5\pm8.8\\ 243.0\\ 252.3\\ 268.7\pm4.5\\ 256.0\\ 249.5\pm11.3 \end{array}$	$181.8 \pm 16.3 \\ 183.0 \\ 187.7 \pm 12.6 \\ 201.7 \\ 191.3 \\ 190.5 \pm 4.9 \\ 187.3 \pm 9.8 \\ 179.0 \\ 183.0 \\ 179.5 \pm 4.3 \\ 206.0 \\ 198.2 \pm 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 \\ 19.4 $
Nyiro (6) S. Guaso Nyiro (3)	578.8 ± 10.5	553.3	328.7	256.0	201.0
2. Other areas Cape (5) S. E. Africa (6) Chobe (4) Zambesi (8) W. Africa (4)	$667.0 \pm 37.7$ $575.2 \pm 8.1$ $615.0 \pm 15.6$ $567.4 \pm 21.8$ $541.3 \pm 17.5$	$606.3 \pm 25.3$ $541.7 \pm 13.6$ $560.0 \pm 8.4$ $553.8 \pm 20.4$ $522.7 \pm 10.8$	$372.5 \pm 13.4$ $330.4 \pm 8.5$ $352.0 \pm 9.9$ $331.1 \pm 17.2$ $324.3 \pm 3.8$	$315.3 \pm 17.6$ $259.2 \pm 11.3$ $282.3 \pm 7.4$ $249.9 \pm 14.4$ $257.5 \pm 3.5$	$\begin{array}{c} 218.8 \pm 23.6 \\ 191.3 \pm 5.8 \\ 197.5 \pm 6.3 \\ 186.6 \pm 12.8 \\ 191.0 \pm 5.5 \end{array}$

additional specimens since the two authors wrote, while in the second case it is likely that only the most important skulls were measured).

With the additional material, a more detailed study becomes possible of the populations of East Africa. Table 1 shows the parameters of thirteen East African "populations", while Fig. 1 indicates their geographical placement. (In some cases, individual skulls were available from other localities; these are marked on the map but not given in the table). The first noticeable thing is that there is a clinal size decrease from west to east, from Karagwe to the Tana river. The two skulls from near Lake Baringo are the largest of all, and the Aberdares and Lakiundu populations are also intermediate. There is much less variation in Basal length than in the Greatest length (Occipitonasal), while fluctuations in the other three measurements seem to be more random. Certain populations stand out in one or two features: the Baringo skulls in their broad zygomata and occiput, and the Tana river ones in their narrowness. The five measurements were the most significant of those from ZUKOWSKY's table; most of the others were only given in a few cases, but some, such as occipital height, though given in the majority of cases, did not add anything.

Concerning the localities "Arusha" and "Kilimanjaro", it must be supposed that these are general areas rather than exact collecting localities. Also the two Guaso Nyiro series, from the Smithsonian Institution, are labelled respectively "Northern Guaso Nyiro, Sotik" and "Southern Guaso Nyiro, Sotik". This is confusing, as the town of Sotik lies considerably west of the Southern Guaso Nyiro, and is nowhere near the Northern Guaso Nyiro. Both indications must remain uncertain for the time being.

### Geographic Variation in the Black Rhinoceros

Applying the "75% of rule"<sup>1</sup>, one finds that the Kiboko, Tsavo and Tana populations are indistinguishable, and that the Karagwe and Serengeti groups are also indistinguishable, but perfectly distinguishable from the first three. We thus have two groups in East Africa, a small and a large one, with the Eyasi, Arusha and Kilimanjaro groups being intermediate. The Baringo skulls are beyond the limits of variability of either of the two groups, and the Lakiundu and Aberdares series are intermediate between Baringo and the Tana group. Turning now to populations outside the East African area, we find that, rather surprisingly, the S.E. African skulls (Natal and Caffraria, indistinguishable on ZUKOWSKY's figures) are not significantly different from the large East African type (Karagwe and Serengeti). The Zambesi skulls show a higher variability than those from other areas; and this is indeed a somewhat heterogeneous category, formed from a series of skulls with no better locality than "Mashonaland" or "Mozambique". The West African skulls are very close to the small East African type, while both the Cape and Chobe skulls are perfectly distinct from all others.



Fig. 1. Diceros bicornis localities in East Africa, referred to in text. Not listed on map: Cherangangi Hills; Archers Post; Longaya water. These localities are a little further north than the limits of the map, the first being near the Uganda border, the other two approximately due north of Mt. Kenya.

<sup>1</sup> See MAYR, LINSLEY & USINGER, 1953, Methods & Principles of Systematic Zoology, p. 146.

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Clearly, we have here the basis of a taxonomic grouping. A single widespread race is indicated, distributed from Transkei in the south to Lake Victoria in the north, with a very large race at the Cape, another rather large one on the Chobe river, two smaller ones respectively in East Africa to the east of the Rift Valley and in West Africa, and a large broad-skulled one to the northwest of the Kenya distribution.

Turning now to ZUKOWSKY's table, one must look for evidence that the other "races" fall into one of these major types, or else form a further type. They may be dealt with one by one.

keitloa. — The single skull attributed to this race is smaller than most of the Cape skulls but considerably larger than the so-called D. b. keitloa var. minor. Its toothrow length, however, comes nearer the latter. Unless it is merely a small-toothed variant of the Cape form, it would seem to make a good intermediate between the Cape and the large Eastern and South-eastern type.

occidentalis. – Apart from a very large zygomatic breadth, the single skull of this form would belong easily with the Eastern and South-eastern type.

angolensis. — These skulls show no difference from the Eastern and South-eastern race. This makes it all the more likely that the broad zygomata of the geographically intervening occidentalis are attributable to individual variation.

rowumae. — This is one of the invalid "Eventualnamen" pointed out by MERTENS. In addition to the type in Berlin, there is also a skull labelled "Rovuma river" in the British Museum. Neither of the two shows any difference from the Eastern and Southeastern race.

*michaeli.* — The Holotype of this subspecies is from "between Engaruka and Serengeti", i. e. in the intergrade zone between the small and large East African races. The type itself, however, agrees on a purely typological basis with the small race.

*rendilis.* – The two Northern Guaso Nyiro specimens agree better with the small East African race, while the Jubaland skull which is attributed to *rendilis* is of the large type.

*ladoensis.* – The Holotype, from Shambe, and a skull in the Smithsonian Institution from Gondokoro, both are strikingly reminiscent, in their broad zygomata and occiput, of the Baringo skulls in Kenya.

somaliensis. – The single skull attributed to this race does not fit clearly into any of the other forms, being especially unique in its very narrow zygomatic breadth. Two subadult skulls in Vienna, from Mersi in Ogaden, agree well with the Somali skull, being (size for size) only a little broader at the zygomata.

brucii and atbarensis. — These two races must be re-shuffled. The two skulls listed as atbarensis are both decidely subadult; on the other hand some of the skulls listed under brucii from "Abyssinia" have a more exact locality. Number 74. 11. 2. 2. is from Cachir Setit, and thus a virtual topotype of brucii; while no. 69. 2. 2. 14 is from Bejuk, Anseba valley, no. 76. 9. 26. 6 is from Atbara river, and no. 79. 11. 29. 4 from Bogos. A further skull from Bogos is in the Cambridge museum. All these last would belong to atbarensis rather than to brucii, and they are indeed — those that are fully adult — a little smaller, but not very markedly, and a size variation covering both supposed races can be found within either of the East African forms. In general, the skulls from Ethiopia are not unlike the Somali and Ogaden skulls, but slightly broader.

Before compiling synonymies and calculating subspecies parameters, one must look at the photographs of rhinoceroses in the flesh, to determine whether any external features seem to characterise one race or another. It is felt by the present author that in characterising the subspecies externally, ZUKOWSKY did not sufficiently take age factors into account, and that such things as depth of skin-folds and costal grooving would be very dependant upon age. None the less three habitus-types do appear distinguishable:

- 1. The general East, South-east and South-west African type, with a short, compact body, well-marked skin-folds and large head.
- 2. The *brucii-atbarensis* type, also the photograph identified as *rendilis* on page 120, with a much longer, more slender body, small head and comparative lack of skinfolds.
- 3. The West-African type, D. b. longipes, with its long legs, smooth skin, short body and characteristic thickened base to the anterior horn.

It may be noted that the external appearance of the Cape and Chobe races is unknown.

The subspecies of *Diceros bicornis* may now be allotted and defined. In the calculation of the parameters (Table 2), all single-specimen localities were allotted on the basis of geography, and it was found that, e. g. the skulls from Taveta and Amboseli were morphologically also of the Kiboko-Tsavo-Tana type. In some cases, however, where a delimitation of range was involved, skulls had to be allotted typologically, e. g. the large size of the skull from Umba steppe was taken to mean that the large East African race encircles the small one to the south.

The subspecies may now be listed as follows, with full synonymy:

1. Diceros bicornis bicornis (Linnaeus, 1758). Cape black rhinoceros.

- 1758: *Rhinoceros bicornis* Linnaeus, Syst. Nat. ed. 10, 1:56. "India" (= Cape of Good Hope according to THOMAS).
- 1803: Rhinoceros africanus Blumenbach, Man. H. N. 1:156. Cape of Good Hope.

# Table 2

# Subspecies of Diceros bicornis: Means and Standard deviations

Measurements of intergrade specimens and populations are given in Table 1

	Greatest length	Basal length	Zygomatic breadth	Toothrow length	Occiput breadth
1. Adult: third n	olars in wear, .	sutures closed			
bicornis (5) chobiensis (4) minor (23) michaeli (22) ladoensis (6) brucii (10) longipes (4)	$\begin{array}{c} 667.0\pm 37.7\\ 615.0\pm 15.6\\ 576.0\pm 17.0\\ 532.6\pm 20.9\\ 597.8\pm 20.9\\ 570.3\pm 18.9\\ 541.3\pm 17.5\end{array}$	$514.2 \pm 14.2$ $557.5 \pm 14.2$	$\begin{array}{r} 330.4 \pm 10.5 \\ 326.8 \pm 9.8 \\ 347.7 \pm 11.2 \\ 315.4 \pm 9.3 \end{array}$	$\begin{array}{c} 315.3 \pm 17.6 \\ 282.3 \pm \ 7.4 \\ 254.1 \pm 13.0 \\ 251.2 \pm 13.1 \\ 253.7 \pm 13.9 \\ 251.4 \pm 13.6 \\ 257.5 \pm \ 3.5 \end{array}$	$\begin{array}{c} 218.8 \pm 23.6 \\ 197.5 \pm \ 6.3 \\ 188.2 \pm 12.1 \\ 186.2 \pm 10.1 \\ 210.2 \pm \ 6.3 \\ 182.5 \pm 10.6 \\ 191.0 \pm \ 5.5 \end{array}$
2. Junadult: third molars just erupted, sutures open					
bicornis (2) minor (2) michaeli (1) ladoensis (2) brucii (1)	577.5 541.5 519 537.5 523	542.0 521.5 503 516.5 502	335.0 313.5 316 324.0 292		196.0 179.0 170 (182) 166
3. Late juvenile: third molars unerupted					
minor (5) michaeli (2) ladoensis (2) brucii (4) longipes (3)	489.4 476.0 501.0 489.3 490.0	503.4 465.0 503.5 462.3 492.3	291.8 298.0 320.0 279.8 294.3		167.8 (166) 164.5 169.7



Fig. 2. Distribution of subspecies of Diceros bicornis

1836: Rhinoceros keitloa A. Smith, Rep. Exped. Expl. C. Africa, 44. "Country north and south of Kurrichaine" (Marico district, W. Transvaal). Although probably an intergrade between this race and *D. b. minor*, this name may be fixed as a synonym of the present race.

- 1837: *Rhinoceros keitloa* A. Smith, Cat. S. Afr. Mus. 7. 180 miles N. E. of Lattakoo (Kuruman).
- 1842: *Rhinoceros bicornis* var. B. *Rhinoceros gordoni* Lesson, Nouv. Tabl. Règne Anim. Mamm., 159. Based on BLAINVILLE's "Rhinoceros de Gordon", from environs of the Cape.
- 1845: Rhinoceros niger Schinz, Synops. Mamm. 2:335. Chuntop (see Zukowsky, p. 50). The specimen quoted by Zukowsky, from near the type locality, has a mandibular length of 520 mm., as big as any Cape specimen.
- 1845: Rhinoceros camperi Schinz, loc. cit. Cape of Good Hope.
- 1898: Rhinoceros bicornis capensis Trouessart, Cat. Mamm. Viv. Foss. 757. Cape.

Distribution: Fish River, Cape of Good Hope, Hottentots River (Beaufort West: an incomplete "pick-up" skull in British Museum), to middle latitudes in Southwest Africa.

- 2. Diceros bicornis chobiensis Zukowsky, 1964.
- 1964: Diceros bicornis chobiensis Zukowsky, Zool. Garten (N. F.) 30:79. Konsumbia, parent-streams of the Loma, tributary of the Cuando, Angola.
- 3. Diceros bicornis minor (Drummond, 1876). Large East and South-East African rhinoceros.
- 1876: Rhinoceros bicornis major & minor Drummond, P. Z. S. 109. R. b. minor ("all country south-east of Zambesi", Zululand selected by ZUKOWSKY) has priority because of selection by ZUKOWSKY as first reviser. R. b. major, from Black Umfolosi to Limpopo.
- 1876: Rhinoceros keitloa Drummond, loc. cit. Black Umfolosi to Limpopo.
- 1893: Rhinoceros holmwoodi Sclater, P. Z. S. 517. Udulia, 50 miles S. of Speke Gulf.
- 1922: Opsiceros occidentalis Zukowsky, Arch. Naturgesch. 88 A, 7:162. Kaokoveld-Kunene region.
- 1947: Diceros bicornis punyana Potter, Field, 190:385. Hluhluwe Game Reserve.
- 1964: Diceros bicornis angolensis Zukowsky, Zool. Garten 30:73. Virui waterhole, Mossamedes, Angola.
- 1964: Diceros bicornis nyasae Zukowsky, loc. cit. 93. North end of L. Nyasa, Karonga, and Niam-niam land, east of L. Rukwa. Invalid; proposed by implication.
- 1964: Diceros bicornis rowumae Zukowsky, loc. cit. 94. Inland from Mikindani. Invalid; proposed by implication.

Note. The theory that two forms of Black Rhinoceros coexist in Southeast Africa is discussed by ZUKOWSKY (pp. 41-5), who recognises a large *D. b. keitloa* (synonym major Drummond) and a small *D. b. keitloa* var. minor (synonym punyana Potter). If two forms do exist side by side, they cannot be conspecific. However Miss ADRIENNE ZIHLMAN was kind enough to make enquiries while in South Africa on my behalf; game wardens, who knew the relevant literature, were unanimous in agreeing that only one form existed. Perhaps there was confusion with pairing of subadult animals; FOSTER (1965) indicates that the probable breeding population starts with animals with third molars only slightly worn, i. e. not full-sized. Accordingly, all three of DRUMMOND's names will refer to this race; which ranges from Transkei and northern S. W. Africa to L. Victoria.

 Diceros bicornis michaeli Zukowsky, 1964. Small East African black rhinoceros.
1964: Diceros bicornis michaeli Zukowsky, Zool. Garten 30:115. Between Engaruka and Serengeti. Although the type locality is in the intergrade zone between

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this race and the last, the skull is typical for the small race; and it is felt apt to continue to honour MICHAEL GRZIMEK, for whom the race is named. 1964: Diceros bicornis rendilis Zukowsky, loc. cit. 122. Northern Guaso Nyiro.

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Distribution: Kenya, east of the Rift valley, into extreme northern Tanzania.

5. Diceros bicornis brucii (Lesson, 1842). Somali black rhinoceros.

- 1842: Rhinocerus bicornis var. A, R. bruccii Lesson, Nouv. Tabl. Regne Anim. Mamm. 159. Based on Blainville's "Rhinoceros de Bruce" from Tscherkin, between Bahr Salaam and Atbara rivers.
- 1870: Rhinoceros keitloa Blanford, Geol. Zool. Abyssinia, 243. Not of A. Smith, 1836.
- 1897: Rhinoceros bicornis somaliensis Potocki, Notatki Mysliwskie z Afryki, 82. Somaliland.
- 1947: Diceros bicornis palustris Benzon, Field, 189:529. Near Aweng, north of Lol river, Bahr-el-Ghazal. Not mentioned by Zuкowsky. Measurements fit well with present race.
- 1964: Diceros bicornis atbarensis Zukowsky, Zool. Garten 30:141. Anseba valley, Eritrea.

Distribution: northern Somalia and Ogaden to Sennaar and Bahr-el-Ghazal district.

- 6. Diceros bicornis ladoensis Zukowsky, 1964.2
- 1914: Diceros bicornis somaliensis J. Allen, Bull. Amer. Mus. N. H. 33: 340. Cherangangi Hills, Kenya, Not of Ротоскі, 1897.
- 1964: Diceros bicornis ladoensis Zukowsky, Zool. Garten, 30:124. Shambe, upper Nile, near Lado. Proposed by implication; invalid (MERTENS, 1966).

Diagnosis: a large race, larger than *minor* but smaller than *chobiensis*, with very broad zygomatic arches and occiput. See Table 2.

- Distribution: Shambe and Gondokoro to Baringo district, thence to L. Naivasha.
- 7. Diceros bicornis longipes Zukowsky, 1949.
- 1949: Diceros bicornis longipes Zukowsky, Arche Noah, 1:16. Mogrum (Chad Republic).

It must be admitted that there is considerable uncertainty in trying to fit clines into a taxonomic scheme. The three-way clinal variation in East Africa between *minor*, *michaeli* and *ladoensis* does, nonetheless, satisfactorily permit the breaking-up of the specimens into three groups – subspecies as above – and their intergrades.

Fig. 1 breaks down taxonomically as follows:

D. b. minor: A, B, C, D, F, L. minor – michaeli intergrades: E, G, H, I, K. D. b. michaeli: J, M, N, O, P, Q, R, S, T. michaeli – ladoensis intergrades: U, V. D. b. ladoensis: W, X, Y, Z.

In addition to those shown on the map, Archers Post and Longaya water are localities for subspecies *michaeli*, and Cherangangi Hills (and Lado and Gondokoro) for *ladoensis*. A skull labelled "Nairobi" – probably a collecting centre rather than

<sup>&</sup>lt;sup>2</sup> The name Diceros bicornis somaliensis J. Allen, 1914, is of course much earlier than ladoensis Zukowsky, 1964; but it is preoccupied by somaliensis Potocki, 1897 — synonym of D. b. brucii according to me, so that ladoensis must remain as the valid name.

an actual locality – is also typical for *ladoensis*. Finally, skulls from Jubaland and from Lamu in Ogaden are intergrades between *michaeli* and *brucii*.

Information on the index-cards of the Powell-Cotton collection gives the shoulderheight of a rhinoceros from East of Lake Baringo as 150 cm. If this is taken by a comparable technique as the measurements for various races given by ZUKOWSKY, this would indicate a small bodily size for a large skulled-animal. From ZUKOWSKY's data it would seem that shoulder heights for other races are as follows:

D. b. bicornis	202—224 cm (2)
D. b. chobiensis	170–173 cm (2)
D. b. minor	137–179 cm (16)
D. b. michaeli	132–153 cm (7)
D. b. brucii	137—142 cm (2)
D. b. longipes	146-147 cm (2) (Powell-Cotton).

#### Summary

The classification of the subspecies of the Black Rhinoceros, *Diceros bicornis*, is reviewed in the light of a re-interpretation of ZUKOWSKY'S (1964) data, with additional data collected by the author. It is concluded that in East Africa there is a size-increase cline from east to west in southern Kenya and northern Tanzania, and another size-increase cline together with marked increase in skull breadth from south-eastern to north-western Kenya. The three extremes are given subspecific rank; one of the three is indistinguishable from specimens in Zambia, Mashonaland, Zululand and Angola. There are two additional subspecies in southern Africa, recognisable by skull characters; while two others, not so easily distinguishable by their skulls but easily characterised externally, inhabit respectively the Somalia-north Sudan region and the Lake Chad area. Synonymy and skull measurements are given; one of ZUKOWSKY's invalid names, *Diceros bicornis ladoensis*, is here used for the first time as the name of a definite race, and so obtains validity.

#### Zusammenfassung

Die Klassifikation der Unterarten des Schwarzen Nashorns, Diceros bicornis, wird nach den Daten von Zukowsky (1964) und zusätzlichen, vom jetzigen Autor gesammelten neu interpretiert. Es ergibt sich, daß in Ostafrika die Größe von Osten nach Westen zunimmt vom südlichen Kenya zum nördlichen Tanzania, und daß sich eine weitere Größenzunahme findet gleichzeitig mit merklicher Breitenzunahme des Schädels — vom südöstlichen nach dem nordwestlichen Kenya. Den drei Extremformen wird subspecifischer Rang zugesprochen. Eine dieser drei Formen ist nicht zu unterscheiden von Exemplaren aus Zambia, Mashonaland, Zululand und Angola. Zwei weitere Subspecies im südlichen Afrika sind durch Schädelmerkmale zu diagnostizieren. Zwei andere, die nach dem Schädel nur schwer, aber nach der äußeren Erscheinung leicht zu unterscheiden sind, bewohnen resp. die Somali-Nordsudan-Region und das Tschadsee-Gebiet. Synonyme und Schädelmessungen werden gegeben. Einer von Zukowskys invaliden Namen, nämlich Diceros bicornis ladoensis, wird hier zum ersten Mal als Name einer definierbaren Rasse benutzt und wird dadurch valide.

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# Die Entwicklung des Brustbeinkammes bei den Fledermäusen

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# Eingang des Ms. 6. 2. 1967

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Die Fledermäuse besitzen, als die einzigen Säugetiere, einen ausgeprägten Brustbeinkamm, der dem der Vögel ähnelt (Abb. 1). Die Ausbildung des Brustbeinkammes hängt zweifellos mit dem Fliegen zusammen, denn er dient als Ursprungsfläche für die mächtigen Flugmuskeln der Musculus-pectoralis-Gruppe. Über die Entstehung und

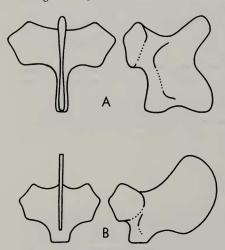


Abb. 1. Manubrium sterni mit Brustbeinkamm bei Rousettus angolenis (A) und Miniopterus schreibersi (B). Links ist die Ventralansicht, rechts die Lateralansicht dargestellt

Formung dieses funktions-, und wie man sehen wird, auch evolutionswichtigen Organs bei den Fledermäusen, ist bisher noch nichts bekannt. Wir hatten die Möglichkeit, die Embryogenese des Brustbeins meist bei fortlaufenden Embryonenserien an zahlreichem Material zu untersuchen. Die vergleichendanatomischen und embryologischen Untersuchungen der Fledermäuse sind nicht nur von morphologischem, sondern auch von evolutionstheoretischem Interesse, wie dies einige ausführliche Arbeiten klar demonstrierten (SITT, 1943; STARCK, 1943; FRICK, 1954; SCHNEIDER, 1957). Die vorliegende kurze Mitteilung will diese außerordentliche Bedeutung der Chiroptera unterstreichen und auf einige neue, unbekannte Entwicklungsvorgänge des Säugetiersternums hinweisen, denn diese sind immer noch unzureichend bekannt, wie aus verschiedenen Arbeiten hervorgeht (GEGENBAUR, 1864; RUGE, 1880; GOETTE, 1887; CARWARDINE, 1893; EGGE-